

Construction costs for some aquatic plants

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Abstract

Resource allocation reflects a plant's response to its environment and affects its overall growth and performance in a particular habitat. We measured ash, C, N, and caloric content for various parts of *Hydrilla verticillata* (L.f.) Royle, *Potamogeton nodosus* Poir., *P. gramineus* L., and *P. pectinatus* L. Mean ash content of vegetative propagules ranged from 2.96 to 5.46%, lower than values previously reported for aquatic plant shoots. *Potamogeton* propagule C and N contents were greater than those of *Hydrilla* propagules. Mean propagule caloric content ranged from 3753 to 4198 cal g⁻¹ and construction costs from 1.00 to 1.12 g glucose g⁻¹. They were similar to or slightly greater than those for shoots or leaves. Construction costs for leaves of eight aquatic species averaged 1.02 g glucose g⁻¹. Vegetative propagules had sink strengths similar to those of shoots. *H. verticillata*, *P. pectinatus*, and *P. gramineus* were grown in a greenhouse with different levels of N in the water column. In this experiment, *P. pectinatus* and *H. verticillata* roots had higher construction costs than shoots whereas *P. gramineus* did not. Only the costs for *P. pectinatus* shoots and roots were affected by the N level in the water column. Construction costs for aquatic plant vegetative propagules, shoots, and roots were lower than similarly calculated values published for roots, stems and leaves of terrestrial plants, in agreement with expectations based on the structural characteristics of leaves and stems of aquatic plants.

Keywords: Construction cost; Heat of combustion; *Hydrilla*; *Potamogeton*; Propagules; Tubers; Turions; Winter buds

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1. Introduction

Resource allocation refers to the distribution in a plant of carbon, nitrogen, and other nutrients among structures which perform different essential functions, such as photosynthesis, nutrient acquisition, or reproduction (Bloom et al., 1985; Lovett-Doust, 1989). The way a plant allocates resources among different organs and different metabolic functions affects its overall growth and performance in a particular habitat (Williams et al., 1987). One approach to understanding resource allocation patterns involves calculating the energy required to construct and maintain a specific tissue. Construction cost has been defined as the amount of glucose required to provide carbon skeletons, reductant, and adenosine 5'-triphosphate (ATP) for the synthesis of organic compounds (Williams et al., 1987), and these estimates thus provide a link between carbon fixation and changes in biomass (Chiariello et al., 1989). Several workers have developed methods for estimating the costs of constructing plant structures (Griffin, 1994). Williams et al. (1987) provided a set of techniques and equations to estimate the construction costs of plants from simple measurements of the heat of combustion, ash content, and organic nitrogen content.

Rooted aquatic plants are important in the structure and functioning of freshwater ecosystems, providing food and cover for animals and influencing the physical and chemical aspects of water and sediment (Carpenter and Lodge, 1986). Compared with terrestrial plants, submersed aquatic plants have decreased proportions of woody tissues in stems, large internal air spaces in the stems, and reduced leaf cuticles (Moss, 1988). These characteristics suggest that construction costs for submersed aquatic plants should differ from those of terrestrial plants, but data that address this question are scarce. In a recent review, Madsen (1991) concluded that resource allocation by submersed macrophytes has received much less attention than that given to terrestrial plants. Griffin (1994) summarized results from several reports on plant construction costs and concluded that there were no estimates for aquatic macrophytes using the methods of Williams et al. (1987).

The purpose of this study is to provide estimates of construction cost for various parts of aquatic plants and to compare them with reported construction costs for similar tissues of terrestrial plants. Because many aquatic plants reproduce principally by vegetative means, rather than by seed (Sculthorpe, 1967), the relative construction costs for perennating propagules and leaf tissue may be important considerations in understanding a species' reproductive success. Values for these construction costs were calculated for a number of representative species. Species were selected using several criteria. Some are troublesome weeds in North America, for instance, the two biotypes of *H. verticillata* (L.f.) Royle, *Egeria densa* Planch., and *Myriophyllum spicatum* L. In other cases leaf type was a criterion. *Eichhornia crassipes* (Mart.) Solms possesses emergent leaves; other plants have submersed (*Zannichellia palustris* L., *E. densa*, *Potamogeton pectinatus* L.) or floating and submersed leaves (*P. gramineus* L. and *P. nodosus* Poir.). Plants possessing a number of propagule types were included to determine if these anatomical differences had a significant effect on construction costs; *Potamogeton* species possess winter buds (*P. gramineus* and *P. nodosus*) or true tubers (*P. pectinatus*) which differ in anatomy and organization from the subterranean and

axillary turions of *H. verticillata*. Finally, the influence of nitrogen nutrition on construction costs was examined for three species under limited conditions.

2. Methods

2.1. Plant material

Potamogeton nodosus winter buds were collected from the Pratt Supply Canal (Richvale Irrigation District, California; Spencer et al., 1992). *P. gramineus* winter buds were collected from the Byrnes canal (Solano Irrigation District, California; Spencer et al., 1992). *P. pectinatus* tubers, and subterranean turions (hereafter tubers) and axillary turions (hereafter turions) of the monoecious and dioecious biotypes of *Hydrilla verticillata* were obtained from cultures at the USDA Aquatic Weed Control Research Laboratory (Davis, California).

Leaves were collected from plants growing in outdoor cultures at the USDA Aquatic Weed Control Laboratory (dioecious *H. verticillata*, *P. pectinatus*, *P. nodosus*, *Myriophyllum spicatum*, *Eichhornia crassipes* and *Egeria densa*) on 3 and 4 September 1995. *Zannichellia palustris* and *P. gramineus* leaves were collected from plants growing in the Byrnes Canal on 4 September 1995. Leaves were dried at 80°C to constant weight and ground by hand.

2.2. Analyses of plant material

Propagules were dried at 80°C for 48 h, and the dry weight was determined (Coombs et al., 1985). Three individual propagules of each species were ground to a fine powder and sub-samples were used to measure the caloric content (heat of combustion) by the adiabatic dynamic method for bomb calorimetry (Parr Instrument Company, 1985). We used a Parr (Moline, IL) Model 1241 calorimeter connected to a Parr 1720 calorimeter controller. Seven additional propagules, for a total of ten for each category, were used to determine ash content by combustion at 550°C (Brower and Zar, 1977). Caloric values are presented on an ash free dry weight (AFDW) basis. An additional set of 17 propagules, for a total of 20, was dried and sub-samples were analyzed for C and N content using a Perkin–Elmer (Norwalk, CT) 2400-CHN elemental analyzer.

2.3. Estimation of nitrate

The methods of estimating construction costs used here assume that organic nitrogen represents the major form of nitrogen in the plant. This assumption is based on studies with terrestrial species but much less is known about relative nitrogen fractions in aquatic plant components. To test this assumption, the level of nitrate in monoecious and dioecious *H. verticillata* tuber extracts was analyzed after reduction to nitrite in the presence of NADH and nitrate reductase from spinach. To provide the latter, spinach leaves (5 g) were ground in 10 ml of 50 mM potassium phosphate, pH 7.8, at 4°C. The extract was centrifuged at 1090 g and the supernatant desalted by passage through

Sephadex G-10. Tuber extracts were prepared by agitating 20 mg of lyophilized tissue in 1.0 ml of 50 mM potassium phosphate, pH 7.8. After 20 min, the mixture was centrifuged at 10 000 *g* and the supernatant assayed for nitrate. The assay contained in 500 μ l: 200 μ l of spinach extract, 200 μ l of tuber extract and NADH at a final concentration of 0.4 mM. The reaction ran for 18 h at room temperature (20°C) in vacuo. Nitrite production was determined by colorimetry (Scholl et al., 1974). Controls were run to establish that tuber extracts did not inhibit spinach nitrate reductase or the colorimetric assay for nitrite. Standards were run with nitrite to determine the minimal amount of the compound which could be determined in this assay.

2.4. Effect of nitrogen in water column on construction costs

Potamogeton gramineus (five plants per treatment), *P. pectinatus* (five plants per treatment) and *H. verticillata* (monoecious biotype, six plants per treatment) were grown in greenhouse cultures for 8 weeks under high and low nitrogen treatments. The low nitrogen treatment consisted of growing plants in modified UC Mix (Spencer and Anderson, 1987) with the medium described by Smart and Barko (1985) devoid of nitrogen for the water phase. The high nitrogen treatment was similar except that Smart and Barko medium with 4.2 mg N l⁻¹ was used for the water column. After 8 weeks the plants were harvested and separated into above- and below-ground portions. The above-ground portion consisted of stems and leaves, designated as shoots in the following. The below-ground portion consisted of roots or combined shoots and rhizomes for species that produced rhizomes. Carbon, nitrogen, caloric content and construction costs were determined as described.

2.5. Calculation of construction costs

Williams et al. (1987) defined construction cost as a measure of the amount of glucose required to provide carbon skeletons, reductant and adenosine 5'-triphosphate (ATP) for the synthesis of organic compounds. The construction costs (CC, g glucose g⁻¹ dry weight) for different types of propagules were estimated from the equation given by Chiariello et al. (1989) based on the method of Williams et al. (1987):

$$CC = \frac{(0.06968\Delta H_c - 0.065)(1 - A) + (kN/14.0067)(180/24)}{\text{efficiency}} \quad (1)$$

where ΔH_c is the heat of combustion (kJ g⁻¹), *A* is the inorganic fraction of the dry weight (roughly the ash fraction), *k* is the oxidation number for nitrogen (−3 for ammonium) and *N* is the nitrogen content (g g⁻¹). Biosynthetic efficiency varies from 0.84 to 0.95 depending on tissue composition (Williams et al., 1987). We used a value of 0.95 for tubers based on values associated with carbohydrate synthesis (Williams et al., 1987) because of the abundance of carbohydrates found in tubers (Miller et al., 1976) and a value of 0.92 for other plant parts.

3. Results

3.1. Composition of leaves and propagules

Mean ash content of vegetative propagules ranged from 2.96 to 5.46% (Table 1). Leaves had greater ash contents (9.29–18.57%, Table 2) than did vegetative propagules. Ash contents for shoots (i.e. samples with leaves and stems combined) were similar (9.03–16.86%, Table 3) to those of leaves. The samples containing roots or roots and rhizomes ranged from 7.96 to 18.18% ash content (Table 3).

For all propagules, C content was between 40.25 and 42.13% (Table 1). Mean C content of leaves ranged from 37.47 to 44.45% (Table 2). Composite samples of shoots ranged from 37.70 to 41.84% C, whereas similar samples from below-ground parts varied from 35.08 to 40.05% (Table 3).

Propagule N content ranged from 1.12 to 2.24% (Table 1). It appeared that, as a group, *Hydrilla* propagules used in this experiment had lower N contents than *Potamogeton* propagules (Table 1). Mean N content for leaves of eight species of aquatic plants collected from several habitats ranged from 1.26 to 4.93% (Table 2). For plants of *P. gramineus*, *P. pectinatus*, and *H. verticillata* grown under low and high levels of N in the water column, shoots had a higher average N content than roots or roots and rhizomes, but the magnitude of the difference was influenced by the N concentration in the water column (Table 3).

There was little evidence that caloric content differed among the tubers, winter buds or axillary and subterranean turions examined in this experiment (Table 4). Caloric content of leaves ranged from a low of 3750 cal g⁻¹ for *E. crassipes* to 4330 cal g⁻¹ for *H. verticillata* (Table 5). In general, the caloric content of the plant fractions measured in the water column N experiments were comparable with those from the field collected leaves (Table 6).

Nitrate was not present in detectable amounts in tubers of *H. verticillata*. Control experiments indicated that 20 nmol of nitrate could be detected in this system. This would correspond to 1.4 µg of nitrate in the 20 mg lyophilized tissue samples used in the assay. This amount of tissue contained 2.8×10^{-4} mg of nitrogen, so the pool size of

Table 1
Ash content (%), carbon content (%) and nitrogen content (%) for selected aquatic plant propagules

Species	Ash content (%)		Carbon content (%)		Nitrogen content (%)	
	Mean	SE	Mean	SE	Mean	SE
<i>Potamogeton nodosus</i>	3.50	0.52	41.30	0.18	2.24	0.09
<i>Potamogeton gramineus</i>	5.33	0.72	41.49	0.19	2.25	0.08
<i>Potamogeton pectinatus</i>	5.03	1.00	42.13	0.08	2.26	0.05
<i>Hydrilla verticillata</i> , tubers (D)	2.96	0.33	40.27	0.16	1.32	0.08
<i>Hydrilla verticillata</i> , turions (D)	5.46	1.82	40.55	0.16	1.37	0.06
<i>Hydrilla verticillata</i> , tubers (M)	3.43	0.28	40.35	0.06	1.12	0.07
<i>Hydrilla verticillata</i> , turions (M)	3.31	0.92	40.25	0.06	1.34	0.10

Ash content is based on ten replications, carbon and nitrogen on 20 replications. D, Dioecious biotype; M, monoecious biotype; SE, standard error.

Table 2

Ash content (%), carbon content (%), and nitrogen content (%) for aquatic plant leaves from outdoor cultures

Species	Ash content (%)		Carbon content (%)		Nitrogen content (%)	
	Mean	SE	Mean	SE	Mean	SE
<i>Potamogeton nodosus</i>	10.39	0.23	43.92	0.21	3.40	0.08
<i>Potamogeton gramineus</i>	14.53	0.15	42.23	0.28	4.93	0.05
<i>Potamogeton pectinatus</i>	12.55	0.40	39.65	0.11	2.30	0.04
<i>Hydrilla verticillata</i> (D)	13.93	0.96	40.16	0.21	3.03	0.08
<i>Eichhornia crassipes</i>	12.77	1.04	38.67	0.79	1.26	0.29
<i>Egeria densa</i>	18.57	0.19	37.47	0.30	3.80	0.03
<i>Zannichellia palustris</i>	9.29	0.09	44.45	0.09	3.44	0.07
<i>Myriophyllum spicatum</i>	15.70	1.86	39.75	0.06	2.12	0.03

Values are the means of five replications. SE, Standard error; D, dioecious biotype of *Hydrilla verticillata*.

Table 3

Ash content (%), carbon content (%), and nitrogen content (%) for aquatic plants cultured with two levels of nitrogen in the water column

Species	Part	Nitrogen added (mg l ⁻¹)	Ash content		Carbon content		Nitrogen content	
			Mean	SE	Mean	SE	Mean	SE
<i>Potamogeton gramineus</i>	shoot	0	11.14	0.45	41.84	0.21	0.99	0.04
	roots	0	10.21	0.72	40.02	0.25	0.75	0.05
	shoots	4.2	9.03	0.52	41.81	0.14	2.36	0.11
	roots	4.2	7.96	0.68	40.05	0.29	1.35	0.05
<i>Potamogeton pectinatus</i>	shoot	0	13.08	1.02	37.73	0.81	1.14	0.05
	roots	0	13.44	0.63	37.43	0.14	1.00	0.05
	shoot	4.2	13.99	0.25	38.86	0.05	3.02	0.13
	roots	4.2	14.96	1.45	38.14	0.55	1.60	0.12
<i>Hydrilla verticillata</i> (monoecious)	shoot	0	9.65	0.66	37.70	0.13	1.09	0.04
	roots	0	14.29	1.34	35.18	0.35	1.32	0.05
	shoot	4.2	16.86	2.07	38.59	0.57	3.94	0.13
	roots	4.2	18.18	1.01	35.08	0.84	2.44	0.08

Values are based on five replications, except for *Hydrilla*, where there were six replications. SE, Standard error.

Table 4

Caloric content and cost of construction for selected aquatic plant propagules

Species	Propagule	Caloric content (cal g ⁻¹ AFDW)		Construction cost (glucose g g ⁻¹)	
		Mean	SE	Mean	SE
<i>Potamogeton nodosus</i>	winter bud	4077	201	1.10	0.006
<i>Potamogeton gramineus</i>	winter bud	4198	135	1.05	0.004
<i>Potamogeton pectinatus</i>	tuber	4041	270	1.08	0.003
<i>Hydrilla verticillata</i> (D)	subterranean turions	3645	281	1.00	0.002
<i>Hydrilla verticillata</i> (D)	axillary turions	3867	135	1.03	0.002
<i>Hydrilla verticillata</i> (M)	subterranean turions	4068	63	1.12	0.003
<i>Hydrilla verticillata</i> (M)	axillary turions	3753	359	1.00	0.002

Values are the means of three replications. D, dioecious biotype; M, monoecious biotype; SE, standard error.

Table 5

Caloric content (cal g^{-1} ash free dry weight (AFDW)) and construction cost (glucose g g^{-1}) for aquatic plant leaves, based on three replications, except for *Eichhornia crassipes*, which had five replications

Species	Caloric content (cal g^{-1} AFDW)		Construction cost (glucose g g^{-1})	
	Mean	SE	Mean	SE
<i>Potamogeton nodosus</i>	4292	132	1.09	0.04
<i>Potamogeton gramineus</i>	4221	105	0.99	0.03
<i>Potamogeton pectinatus</i>	4270	114	1.07	0.03
<i>Hydrilla verticillata</i> (D)	4330	78	1.07	0.03
<i>Eichhornia crassipes</i>	3750	91	0.95	0.03
<i>Egeria densa</i>	4450	70	1.02	0.02
<i>Zannichellia palustris</i>	4068	60	1.04	0.02
<i>Myriophyllum spicatum</i>	4002	40	1.01	0.01
Overall mean	4140	54	1.02	0.01

SE, Standard error; D, dioecious biotype of *Hydrilla verticillata*.

nitrate must be less than 0.5% of the total nitrogen. Construction cost analyses are conducted as if the nitrogen in the tissue is entirely organic.

3.2. Construction costs

Cost of construction for propagules ranged from 1.00 to 1.12 g glucose g^{-1} . The mean cost of construction for *Hydrilla* propagules was 1.04 g glucose g^{-1} (95% confidence intervals were 0.95–1.13). Propagules of the *Potamogeton* spp. required 1.08 g glucose g^{-1} on average (95% confidence intervals were 1.02–1.14). Overlap of

Table 6

Caloric contents (cal g^{-1} AFDW) and construction cost (glucose g g^{-1}) for aquatic plants cultured at two levels of nitrogen in the water column

Species	Part	Nitrogen added (mg l^{-1})	Caloric content		Construction cost	
			Mean	SE	Mean	SE
<i>Potamogeton gramineus</i>	shoot	0	4089	30	1.07	0.01
	roots	0	3957	58	1.04	0.02
	shoot	4.2	3836	144	0.99	0.04
	roots	4.2	3932	298	1.06	0.09
<i>Potamogeton pectinatus</i>	shoot	0	4235	48	1.08	0.01
	roots	0	4523	107	1.16	0.03
	shoot	4.2	4265	58	1.04	0.02
	roots	4.2	4375	42	1.11	0.01
<i>Hydrilla verticillata</i> (M)	shoot	0	3936	45	1.04	0.01
	roots	0	4299	52	1.08	0.01
	shoot	4.2	4339	55	1.02	0.01
	roots	4.2	4607	57	1.09	0.01

Values are based on five replications, except for *Hydrilla*, where there were six replications. SE, Standard error; M, monoecious biotype.

Table 7

Estimated cost of construction for foliage of submersed aquatic plants based on data from the literature

Species	N (%)	Ash (%)	Caloric content (cal g ⁻¹ AFDW)	Construction cost (glucose g g ⁻¹)	Reference
<i>Potamogeton nodosus</i>	1.79	10.9	4231	1.10	Boyd (1968)
<i>Potamogeton crispus</i>	1.74	16.0	4298	1.05	Boyd (1968)
<i>Potamogeton pectinatus</i>	2.13	13.3	4313	1.09	Sugden (1973)
<i>Potamogeton pusillus</i>	2.19	16.6	4784	1.17	Sugden (1973)
<i>Hydrilla verticillata</i>	2.88	28.0	4791	0.99	Boyd (1969)

Construction cost was calculated using Eq. (1).

confidence intervals suggests that, based on the present data, there is no statistical evidence for a difference between the cost of construction for *Hydrilla* and *Potamogeton* propagules. Mean construction cost of leaves varied from 0.95 g glucose g⁻¹ for *E. crassipes* to 1.09 g glucose g⁻¹ for *P. nodosus* (Table 5).

In the water column N experiment, construction costs for roots were greater than for shoots in the case of *P. pectinatus* and *H. verticillata* (ANOVA; $P < 0.05$). No significant differences (ANOVA; $P > 0.05$) were observed for *P. gramineus* (Table 6). Differences in construction costs related to nitrogen level in the water column were only significant for *P. pectinatus* (ANOVA; $P < 0.05$). Construction costs for aquatic plant shoots, and roots and rhizomes for the plants in this experiment were within the range of those for leaves or propagules collected from natural habitats as calculated from data reported in the literature (Table 7).

4. Discussion

4.1. Ash content

Ash contents of vegetative propagules (Table 1) were similar to data reported for *P. pectinatus* tubers, which ranged from 5.1 to 5.8% ash content (Anderson and Low, 1976). Vegetative propagules had lower ash contents than shoots of submersed aquatic plants. Samples of leaves and shoots had lower ash contents than reported for foliage of *P. pectinatus*, which Anderson and Low (1976) reported to have between 23.6 and 43.7% ash. However, our data were similar to those of others. Cummins and Wuycheck (1971) reported that ash content for shoots of nine species of submersed aquatic plants ranged from 11.6 to 25%. Sugden (1973) reported that *P. pectinatus* foliage was 13.3% ash and *P. pusillus* foliage ranged from 7.3 to 16.6% ash. Boyd (1968) reported that the ash content of shoots of 12 species of submersed aquatic plants ranged from 9.6 to 40.6% with a mean value of 18.4%. *P. nodosus* shoots had an ash content of 10.9% (Boyd, 1968), very similar to that reported here for that plant. *Hydrilla* shoots were reported to have 28% ash content (Boyd, 1969), about twice the value observed for *Hydrilla* in these experiments. The high literature values for ash contents of shoots may be partly due to different culture conditions. It is known that ash content of plants grown

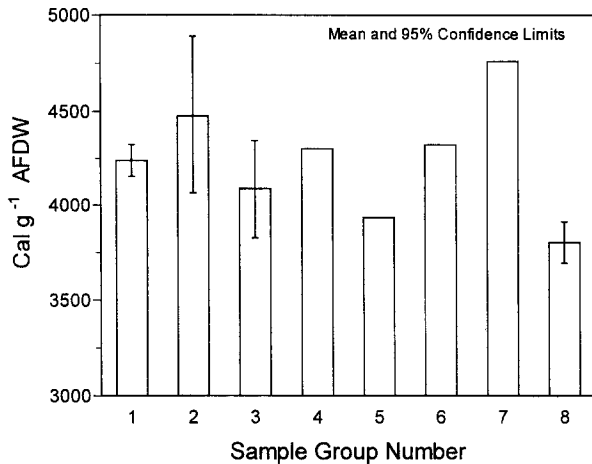


Fig. 1. Mean values for construction costs (in cal g^{-1} AFDW) for propagules, leaves and shoots of *Potamogeton* and *Hydrilla*. The plant material and sources for the values are: 1, *Potamogeton* leaves, Table 5; 2, *Potamogeton* shoots, calculated from the published composition, Table 7; 3, *Potamogeton* propagules, Table 4; 4, *Hydrilla* leaves, Table 5; 5, *Hydrilla* leaves grown with no N added to the water column, Table 6; 6, *Hydrilla* leaves grown with 4.2 mg N l^{-1} added to the water column, Table 6; 7, *Hydrilla* shoots, calculated from the published composition, Table 7; 8, *Hydrilla* propagules, Table 4.

in hard waters may be affected by the precipitation of calcium carbonate during photosynthesis (Vollenweider, 1974). The origins of the differences in ash content in this experiment may be speculated upon. The plants were grown in water of moderate hardness under the same conditions of light and temperature, so differences presumably reflect differences in the balance between photosynthetic rate and respiration under these conditions. A systematic study of these factors needs to be carried out before conclusions are drawn, as the accumulation of marl may have multifaceted effects, e.g. it may protect a plant from herbivory while reducing photosynthetic capacity by light scattering.

4.2. Caloric content

The results for calculations on caloric contents of leaves, shoots, and propagules of *Potamogeton* species and *Hydrilla* are summarized in Fig. 1. Data are included from this experiment, as well as the literature: values are given as means, with 95% confidence intervals when data from several species or different propagule types have been combined. The caloric content of *Potamogeton* or *Hydrilla* propagules in this experiment was less than the value of 4990 cal g^{-1} reported for *P. pusillus* winter buds by Sugden (1973). These results indicate that propagules and leaves of these aquatic plants have approximately equivalent caloric contents. The literature value for the caloric content of *Hydrilla* shoots, 4791 cal g^{-1} AFDW (Table 7), is higher than the values determined in this experiment, but this value may depend on nutritional conditions or other factors not investigated here. In the experiment on the effect of nitrogen in

the water column on characteristics of *Hydrilla* shoots, the increased concentration of organic nitrogen in the leaves of *Hydrilla* and *P. pectinatus* may have been accompanied by an increase in starch content owing to increased photosynthetic activity of the tissue. A similar effect of nitrogen nutrition has been noted on nitrogen content and construction costs in leaves of *Sorghum* (Lafitte and Loomis, 1988). Further experiments need to be conducted to understand the interactions among nitrogen nutrition, construction costs, and photosynthetic and growth rates in aquatic macrophytes.

4.3. Construction costs from literature data

Table 7 provides literature data on the N and caloric content of *Potamogeton* and *Hydrilla* shoots. Costs of construction calculated from these data indicate that on average *Potamogeton* foliage required 1.10 g of glucose for each gram of shoot (95% confidence intervals were 1.03–1.18). The single measurement of *Hydrilla* foliage provides an estimate of 0.99 g of glucose for each gram of shoot. These values are similar to those measured for leaves and shoots in this study (Tables 5 and 6).

5. Conclusions

The cost of construction for *Potamogeton* and *Hydrilla* shoots is similar to or slightly lower than those for vegetative propagules. Propagules would thus be expected to be sinks for photosynthate that are nearly equal to, if not greater than shoots, and this may account for the decline in shoot biomass for plants exposed to conditions which favor propagule production (Spencer and Anderson, 1987; Spencer et al., 1994a, Spencer et al., 1994b).

To our knowledge, this is the first report of construction costs for aquatic plants using the method of Williams et al. (1987). Aquatic plant shoot and propagule costs of construction are lower than the mean values for leaves, stems, and roots from 97 samples of terrestrial plants, estimated by the same procedures and summarized by Griffin (1994). Based on these data, Griffin (1994) concluded that leaves of terrestrial plants had greater construction costs, with a mean value of $1.54 \text{ g glucose g}^{-1}$, than roots or non-photosynthetic stems ($1.34 \text{ g glucose g}^{-1}$ and $1.32 \text{ g glucose g}^{-1}$, respectively), presumably owing to the presence of the photosynthetic apparatus and perhaps high energy compounds, such as cuticular waxes, in the leaves. From the experiments reported here, aquatic plant shoots and vegetative propagules had construction costs which were less than those for any parts of terrestrial plants (Griffin, 1994). These differences may reflect the lack in aquatic plants of both lignified structures, and structures and materials to inhibit water loss (Sculthorpe, 1967). The leaf construction cost for *E. crassipes*, which has emergent foliage, was similar to those for submersed leaves of other species. This may reflect the fact that little investment need be made by this plant to protect against water loss. The low construction cost may also contribute to the weedy habit of this plant, allowing it to occupy a large surface area at relatively low costs.

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